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RE-INVESTIGATION OF ENIGMATIC FISH BONES KNOWN AS COLOBODONTID/PERLEIDID TOOTHPLATES FROM THE UPPER TRIASSIC CHINLE GROUP (SOUTHWESTERN U.S.A.)

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Abstract—A representative selection of enigmatic denticulate/dentigerous plates from the Chinle Group previously assigned to Colobodontidae or Perleididae ("Perleidiformes": Actinopterygii) were reinvestigated and compared to purportedly similar remains of diverse provenance and known identity. The histology of these isolated elements and fragments was also investigated to re-evaluate the former identifications and the tooth-like remains are compared to other Permo-Triassic fish groups. None of the fossils studied can be positively identified as a (crushing) toothplate of a colobodontid or a perleidid. Instead, our preliminary morpho-histologic investigation suggests that the majority of remains do not represent toothplates – despite the denticles' striking similarity with crushing teeth. Most fragments represent denticulate dermal bone with a unique histology belonging to as-yet unidentified osteichthyans. Most purported "molariform teeth" from the Upper Triassic of the American Southwest are therefore interpreted as multiple series of dermal denticles and there is no evidence in these strata of "colobodontids" or "perleidids," groups that were widely distributed during the Early-Middle Triassic.

INTRODUCTION AND HISTORIC BACKGROUND

The Upper Triassic Chinle Group in the western United States is known primarily for its rich paleontological record, especially of petrified wood (e.g., Daugherty, 1934, 1941; Ash and Creber, 2000 and references cited therein) and tetrapod vertebrates (e.g., Long and Murry, 1995; Heckert and Lucas, 2002a, and references cited therein). Less well-known, but still substantial, are the fish faunas of non-tetrapod vertebrates, including both freshwater sharks and diverse osteichthyans (reviewed by Huber et al., 1993; see also Johnson et al., 2002).

An excellent but preliminary survey dealing with the most completely preserved fish taxa from several Chinle localities was provided by Schaeffer (1967). However, he refrained from describing the abundant but more fragmentary material. Schaeffer (1967, p. 326-336) pointed out that the presence of several fish taxa, in particular certain species of semionotids, some redfieldiids (i.e., *Synorichthys*), and the genus *Colobodus* might be verified with larger samples. Subsequent decades of extensive fieldwork have yielded a wealth of new information on the presence and probable abundance of many fishes, (see Jacobs and Murry, 1980; Murry, 1982, 1986; Hunt and Lucas, 1989; Kirby, 1991; Hunt, 1994, 1997, 2001; Heckert, 2001, 2004). There are relatively few localities that yield complete osteichthyan skeletons (Schaeffer, 1967; Johnson et al., 2002), and these generally yield faunas dominated by palaeoniscoids, redfieldiids, and semionotids with rarer coelacanths (Huber et al., 1993; Johnson et al., 2002). Consequently, much of the record of other Chinle osteichthyan taxa has come from fragmentary remains recovered during screenwashing or incidentally in the collection of tetrapods.

Murry (1982, 1986, 1989a, b) gave the first accounts of purported colobodontid tooth plates in the Chinle/Dockum Group and identified 3 tooth types occurring in several localities (i.e., lower Kalgary, Otis Chalk, St. Johns (Arizona), and Rotten Hill; see Murry, 1982). Tooth type 1 consists of "low blunt teeth" that are ornamented and "similar to *Colobodus*," tooth type 2 is "strongly heterodont" and "unornamented," purportedly similar to "*Perleidus*" and other "perleidid" fishes, and tooth type 3 consists of bicuspid teeth purportedly similar to "Colobodontidae." Lacking sound comparative material, Murry (1982) restricted himself to identification of specimens (to *Colobodus* sp.) and discussion of possible phylogenetic relationships of colobodontids. Huber et al. (1993) reviewed the record of fishes in the Chinle and considered most of Murry's material to comprise indeterminate perleidids. Kaye and Padian (1994) also reported "colobodontid" teeth in the highly fossiliferous *Placerias* Quarry ("St. Johns" of Murry, 1986) but stated that many taxa (fish and reptile) may not be "clearly identifiable."

Hunt (1997, 2001) reconsidered the fish fauna from the Upper Triassic Chinle Group from the western U.S.A. and concluded that the enigmatic "phyllodont tooth plates" (see Estes, 1969a) may tentatively be assigned to ?Colobodontidae Andersson, 1916, on the basis of "multiple, superposed sets of replacement teeth." However, he understood perleidids as a synonym of colobodontids, complicating Murry's (1982) concept of tooth types. Heckert (2001) reported the presence of similar dentigerous tooth plates in several localities but did not find any scales to support Murry's identification. The complete absence of colobodontid scales in the Chinle/Dockum Group is remarkable, especially given that scales have usually been reported from Middle Triassic sites where unequivocal tooth plates of colobodontids have been found (Mutter, 2002). Heckert (2004) thus was more circumspect in his assessment of fish diversity, pending the outcome of the project we report here. There is no question that there are numerous "tooth plates" or "phyllodont" (numerous replacement teeth) specimens in the Chinle Group. This paper reports on the affinities of a representative selection of these enigmatic remains.

Estes (1969a) demonstrated that at least eight lineages of albuloid teleosts have "phyllodont teeth," and Johnson and Zidek (1981) described platysomid tooth plates from the Late Permian showing similar histology in this respect. Tooth plates containing numerous tiny (0.05-2 mm), superficially similar "phyllodont teeth" are common microvertebrate fossils from the Chinle Group. Most workers have assigned Chinle specimens to either the Perleididae (Murry, 1982, 1986, 1989a, b; Huber et al., 1993) or Colobodontidae (Hunt, 1994, 2001) based on external morphology. Before Gardiner (1993) synonymized Perleididae and Colobodontidae, both families had been tacitly accepted as synonyms by many paleoichthyologists, but in fact their names only share a jumbled research history (Mutter, 2001, 2004).

With respect to dentigerous bones and teeth described or listed under the name "*Colobodus*" however, subsequent studies did not further appraise the morphological similarity to teeth of *Colobodus* from Middle Triassic Tethyan localities in central Europe. Recent review of the family Colobodontidae (Mutter, 2004) allows critical re-evaluation of these enigmatic Chinle remains. In particular, we attempt here to use

histological features in addition to external morphology for identification of these enigmatic remains.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY; ETHZ, Eidgenössische Technische Hochschule der Universität Zürich, Zürich, CH; GNAUF, Department of Geology, Northern Arizona University, Flagstaff, AZ; MCZHU, Museum of Comparative Zoology, Harvard University, Cambridge, MA; NMMNH, New Mexico Museum of Natural History, Albuquerque, NM; OUSM, Stovall Museum of Science and History, University of Oklahoma, Norman, OK; PEFO and PFV, Petrified Forest National Park Museum, Petrified Forest, Arizona, AZ; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, CH; UAEAS, University of Alberta Earth and Atmospheric Sciences; UALVP, University of Alberta Laboratory for Vertebrate Paleontology (both Edmonton AB, Canada).

GEOLOGIC SETTING

The specimens examined are purported "colobodontid" fossils from the Chinle Group. Most are fragmentary toothplates or dentigerous plates, many obtained by screenwashing, each with numerous small "phyllodont teeth" (see description of specimens). We studied specimens from the Garita Creek, Tecovas, Petrified Forest, and Bull Canyon formations in Texas, New Mexico, and Arizona, U.S.A. (Fig. 1). In the following paragraphs, we provide a brief synopsis of the provenance, including the stratigraphy and age, for each of these sites. Because of the difficulty in correlating nonmarine vertebrate localities to the marine-based timescale, we use the land-vertebrate faunachrons (lvfs) of Lucas and Hunt (1993; see also Lucas, 1998) for the Chinle Group. These include the Otischalkian (early to late Carnian), Adamanian (late Carnian), and Revueltian (early-mid Norian) lvfs.

The stratigraphically lowest locality is the "lower Kalgary" microvertebrate site in Crosby County, Texas, first studied by Murry (1982, 1986, 1989a) (Fig. 2). This site, NMMNH locality 1312, is stratigraphically low in the Tecovas Formation, just a few meters above the base of the Chinle (Camp Springs Formation) in west Texas. Tetrapods collected in the vicinity of Kalgary indicate an Adamanian age for the Tecovas Formation generally (e.g., Lucas and Hunt, 1993), but the lower Kalgary site is so stratigraphically low it must surely represent either late Otischalkian or earliest Adamanian time (Heckert, 2001, 2004).

The nearby upper Kalgary microvertebrate locality is only a few hundred meters to the south and slightly higher stratigraphically (Fig. 2; Heckert, 2001, 2004). This is the type locality of *Adelobasileus cromptoni* Lucas and Hunt, 1990 (Lucas and Luo, 1993), the oldest mammal. Much of the Tecovas Formation, including sites in this area at this level, yields a typical Adamanian fauna of the phytosaur *Rutiodon* (= *Leptosuchus*) and the aetosaur *Stagonolepis* (Lucas and Hunt, 1993; Lucas et al., 1994).

The single specimen from the Garita Creek Formation in Santa Fe County, north-central New Mexico, was recovered from a plaster jacket from the original Lamy bonebed that yielded abundant metoposaurs of the genus *Buettneria* (Romer, 1939; Hunt and Lucas, 1995; Rinehart et al., 2001). The Garita Creek Formation yields an Adamanian tetrapod fauna, including the phytosaur *Rutiodon* and the aetosaurs *Stagonolepis* and *Desmatosuchus haplocerus* (Hunt and Lucas, 1995; Lucas et al., 2001).

Another Adamanian locality, the Dying Grounds locality (Apache County, Arizona, PFV 122), is the only non-NMMNH locality in our study (in the Petrified Forest National Park [PEFO] see Murry and Long, 1989). Dying Grounds is stratigraphically high in the Blue Mesa Member of the Petrified Forest Formation and provided an extraordinarily rich tetrapod fauna first published by Camp (1930). In addition to the extensive macrovertebrate tetrapod collections from this area (Long and Murry, 1995), both Murry (1989b) and Heckert (2001, 2004) have collected diverse microvertebrate faunas from the Dying Grounds. This site and a suite of closely spaced localities yielded the type fauna of the Adamanian lvf (Lucas and Hunt, 1993; Lucas, 1998; Heckert and Lucas, 2002b; Parker, 2002). It is also one of the stratigraphically highest Adamanian localities known, and thus almost surely represents a late interval of Adamanian time (Heckert, 2001, 2004).

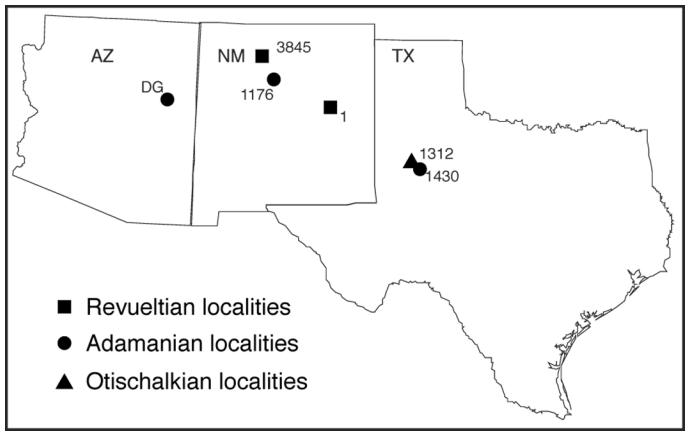

FIGURE 1. Geographic distribution and stratigraphic level of the specimens studied. Localities in descending stratigraphic order: loc. 1 = locality NMMNH 3845 (NM); loc. 2 = locality NMMNH 0001 (NM); loc. 3 = locality PEFO Dying Grounds (AZ); loc. 4 = locality NMMNH 1176 (NM); loc. 5 = locality NMMNH 1430 (TX); loc. 6 = locality NMMNH 1312 (TX). Abbreviations: AZ, Arizona; NM, New Mexico; TX, Texas.

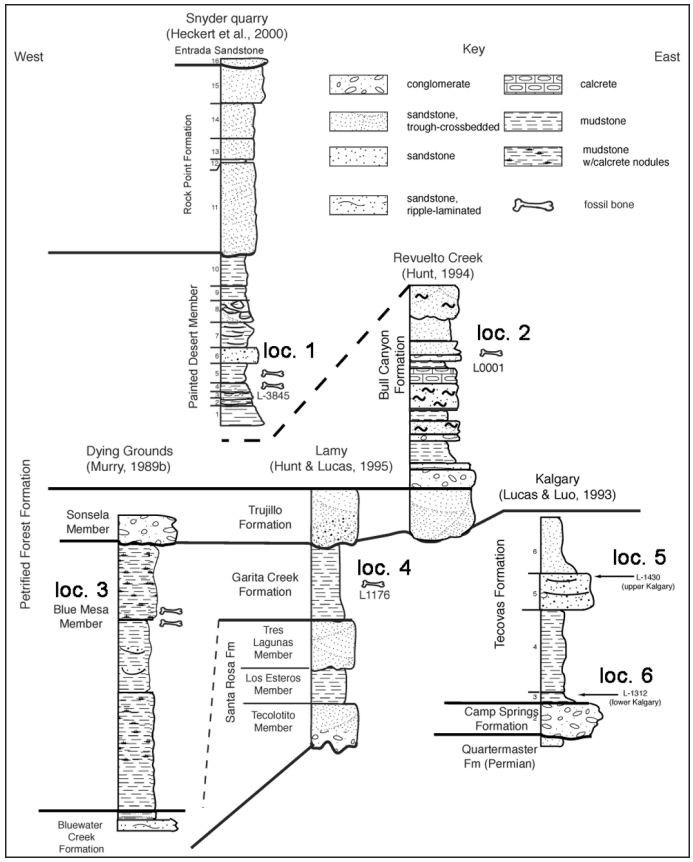

FIGURE 2. Generalized stratigraphic correlation of the fossiliferous localities studied here. See Figure 1 for section locations.

The stratigraphically lowest Revueltian locality we studied was NMMNH locality 1 in the Revuelto Creek badlands in Quay County, east-central New Mexico (Fig. 1). This extremely rich locality is low in the Bull Canyon Formation (Hunt, 1994, 2001) and has yielded the type fauna of the Revueltian lvf (Lucas and Hunt, 1993; Lucas, 1998; Hunt,

2001). It is the type locality of the coelacanth *Quayia zideki* Hunt, 1997. The Revuelto Creek fauna is also the type fauna of Hunt's (2001) Barrancan sub-lvf, although Heckert and Lucas (2002b) noted the difficulty in utilizing sub-lvfs for the Revueltian at this time.

The stratigraphically highest locality from which we examined specimens is the Snyder quarry in Rio Arriba county, north-central New Mexico (Fig. 2). This locality is stratigraphically high in the Painted Desert Member of the Petrified Forest Formation (Heckert et al., 2000; Heckert and Jenkins, 2005). This site yields abundant macrovertebrate fossils, principally of phytosaurs and aetosaurs, but also of dinosaurs and other taxa. Recently, Heckert and Jenkins (2005) described a diverse microvertebrate assemblage from the quarry, including osteichthyan toothplates that we restudy here. The presence of the aetosaur *Typothorax coccinarum* and the phytosaur *Pseudopalatus* indicate a Revueltian age (Zeigler et al., 2003 and references therein).

The specimens investigated in this study are diverse. Some fragments share the same specimen number but may well represent different taxa, once a reliable taxonomic framework is in place. We therefore discuss the evidence with regard to its provenance rather than by referral to preliminary assignments.

MATERIAL AND METHODS

We examined a stratigraphically representative sample of purported "colobodontid/perleidid tooth plates" from strata of the Upper Triassic Chinle Group in the southwestern U.S.A. from the following localities:

1. Snyder quarry, NMMNH locality 3845, Painted Desert Member, Petrified Forest Formation (Revueltian), Rio Arriba County, New Mexico: NMMNH P-33113, P-40287, P-40322 (40322a = thin section), P-40323.

2. Revuelto Creek badlands, NMMNH locality 1, Bull Canyon Formation (early Revueltian), Quay County, New Mexico: NMMNH P-4324, P-4685 (= thin sections P-37820a/b), P-4850.

3. Dying Grounds, PFV-122, Blue Mesa Member, Petrified Forest Formation (late Adamanian), Petrified Forest National Park, Apache County, Arizona: PEFO-20346, PEFO-20401, PEFO-20414, PEFO-20415, PEFO-20416 (thin section P-20416a).

4. Lamy Bonebed, NMMNH locality 1176, Garita Creek Formation (Adamanian), Santa Fe County, New Mexico: NMMNH P-34232. No thin section was made.

5. Upper Kalgary, NMMNH locality 1430, Tecovas Formation (Adamanian), Crosby County, Texas: NMMNH P-26375, P-26376-26386. No thin section was made.

6. Lower Kalgary, NMMNH locality 1312, Tecovas Formation (late Otischalkian/early Adamanian), Crosby County, Texas: NMMNH P-29439, P-29440, P-30781, P-34170, P-34189 (= thin sections P-34189a-j, P-37821a/b, P-37822a/b), P-34190, P-34398.

These specimens were then compared to a variety of representative colobodontids and other taxa, including: Colobodontidae gen. et sp. nov. (PIMUZ T 588); *Colobodus* cf. *bassanii* (PIMUZ T 3010); *Colobodus* sp. nov. (see Mutter, 2002: PIMUZ T 24, thin sections P II 012, P II 013); *Colobodus* sp. (PIMUZ T 1710 (thin section 1), T 2500, T 2504, T 2540 (thin sections 1, 2), T 5253 (thin section P II 014)); Coelacanthidae gen. et sp. indet. (AMNH 11702, 11703, 11704, PIMUZ T 1327 (thin section P II 039); *Whiteia* sp. (UALVP 19245, 46583 [thin sections T-1-T12]); *Spermatodus* sp. (AMNH 4612); *Bobasatrania* sp. (SMNS 56943/thin section 1, SMNS 59184/thin section 1), SMNS 59185, SMNS 87971, UALVP 46494 (thin section T1), UALVP 46646).

All AMNH specimens are from the Permian of Lawn (Texas) except AMNH 4612 (Lower Permian; Admiral/Admiral Belle Plains, near Lake Kickapoo Archer County, Texas, U.S.A.). All PIMUZ specimens are from the Middle Triassic Besano Formation (= Grenzbitumenzone: Anisian/Ladinian boundary), near Meride, Canton Tessin, Switzerland. SMNS specimens are from the Muschelkalk mo3, boundary bonebed (Vaihingen/Enz: 56943; Zwingelhausen: 59184-5, 87971). All UALVP specimens are from the Early Triassic Sulphur Mountain Formation, Vega-Phroso Siltstone Member (probably lower Smithian).

Methods

Wet polishing was accomplished using corundum powder 1-5µm grain size in paraffin for either side of aforementioned ultra thin sections, embedding and gluing with resin. If necessary, evacuation of air took place several times in the evacuator, and heating temperature was between 70 and 80 degrees Celsius for one hour. Precise cuts were obtained using Buehler wafering diamond blades. SiC (grain size 600/800/1200) or preferably Al_2O_3 (grain size 800/1200) was used for sliding. Specimens NMMNH P-4685, P-34189 and UALVP 19245 (uncoated) were briefly etched with 10% hydrochloric acid and subjected to scanning electron microscopy.

DESCRIPTION OF SPECIMENS

Locality 1: The Snyder Quarry

Two specimens (NMMNH P-33113, P-40322, Fig. 3) have been examined in detail from this youngest locality (L-3845). The conical denticles or tubercles usually share a stellate ornament with "crushing teeth" and are widely spaced (but see Fig. 3.3). A thin section through the thin dentigerous plate NMMNH P-40322 reveals the dentigerous portion of the bone consists of a single layer of internally more densely set teeth, anchored in highly vascularized bone. The zone of tooth proliferation is distinctly separate from laminar bone. The pulp cavities are comparatively very large, correlated to tooth size, and single-tooth histology matches the condition observed in all other enigmatic denticulate plates from the Chinle Group (NMMNH P-40322a, Fig. 3.2). The shape and the arrangement of teeth in the second plate (specimen NMMNH P-33113, Fig. 3.3) is very different but also not reminiscent of functional teeth. The denticles are less cone-shaped, blunt and smooth. Numerous pores are visible between the denticles.

Locality 2: Type Revueltian Assemblage (Revuelto Creek)

The specimens from this locality include fragmentary tooth plates, typically bearing asymmetrical or apically recurved teeth, some of which are elongate. On the whole, they are very different from colobodontid teeth in the shape of crown, tooth arrangement and absence of an apical wart. A single specimen (NMMNH P-4685, Fig. 4.1-4.2) is more completely preserved and most likely represents the antero-middle portion of a parasphenoid of the coelacanth *Quayia zideki* Hunt, 1997. This bone's convex dorsal surface is smooth apart from longitudinal, faint grooves. The ventral surface is covered with a shagreen of tiny, delicately striated teeth (Fig. 4.1), variable in shape and often slender-oblong, and the structure of the bone is rather "spongy" revealing large vascular canals (Fig. 4.2). In these respects, the specimen resembles a larger denticulate bone fragment of specimen NMMNH P-34189 from the Tecovas Formation (locality 5, discussion of thin sections below). However, its ornamented teeth measure almost 10 times (2 mm) the size of those of NMMNH P-34189.

The thin section (NMMNH P-37820, Fig. 4.3) reveals that the base of the bone is highly vascularized and contains large cavities with relatively larger teeth than in denticulate plates from the Tecovas Formation (specimens NMMNH P-37821 and P-37822). It is separated from the zone of tooth proliferation by a distinctive lamina. No replacement teeth are present. All teeth (large distal and smaller mesial ones) exhibit an extraordinarily large pulp cavity that "pierces" the thick orthodentine layer and is subdivided by conspicuous series of incremental lines. Osteocyte cell-spaces are absent or at least barely detectable, as in *Whiteia* (see below). The enamel layer is relatively thin with faint, irregular basal lines (detectable under SEM), and no acrodin is present.

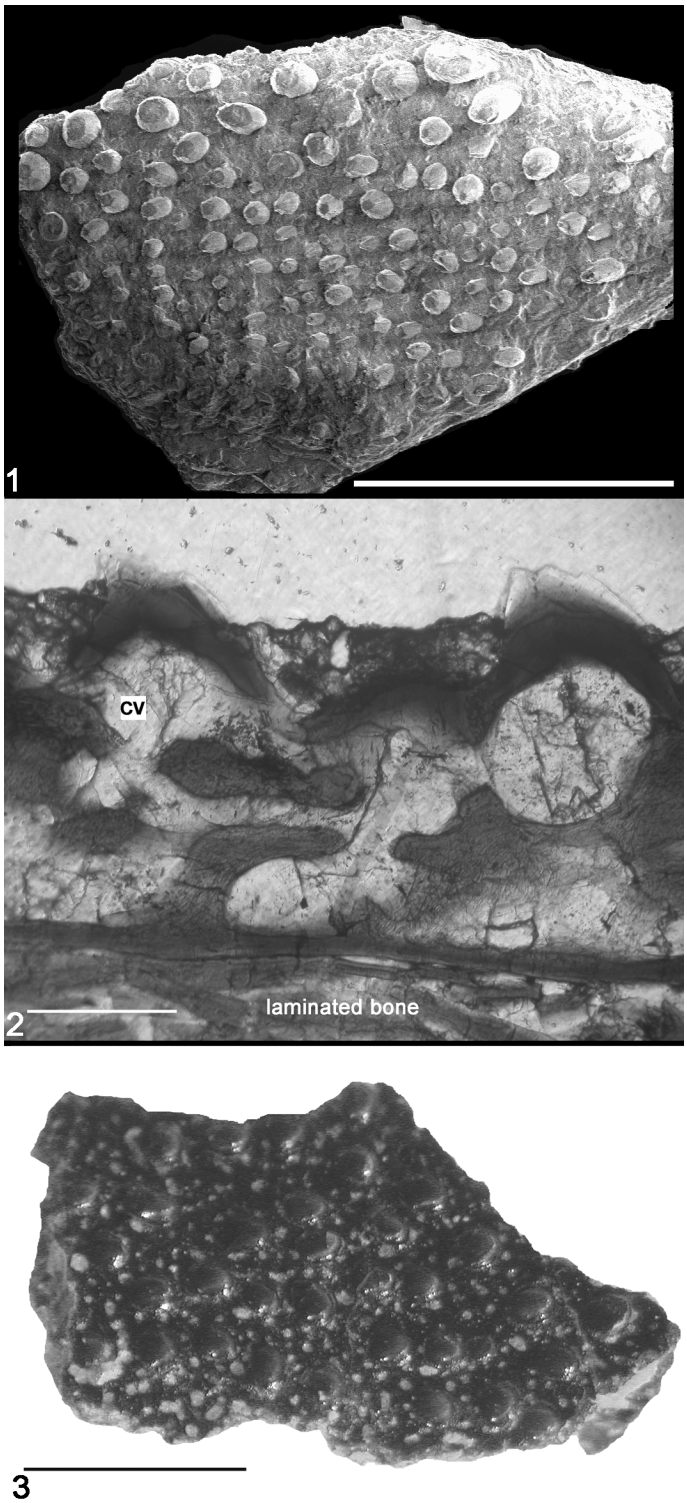

FIGURE 3. Fossils from NMMNH locality 3845 (locality 1 of this study). **1,** Specimen NMMNH P-40322; denticulate plate in occlusal view showing conical denticles with stellate ornament. **2,** Thin section of specimen NMMNH P-40322(a). Note the single "tooth row" clearly separated from the laminated bone. **3,** Specimen NMMNH P-33113, a denticulate plate in occlusal view: the denticles are entirely smooth in contrast to (**1**). Abbreviation: cv, cavity. Scale bars = 2 mm (except 2: 100 μm).

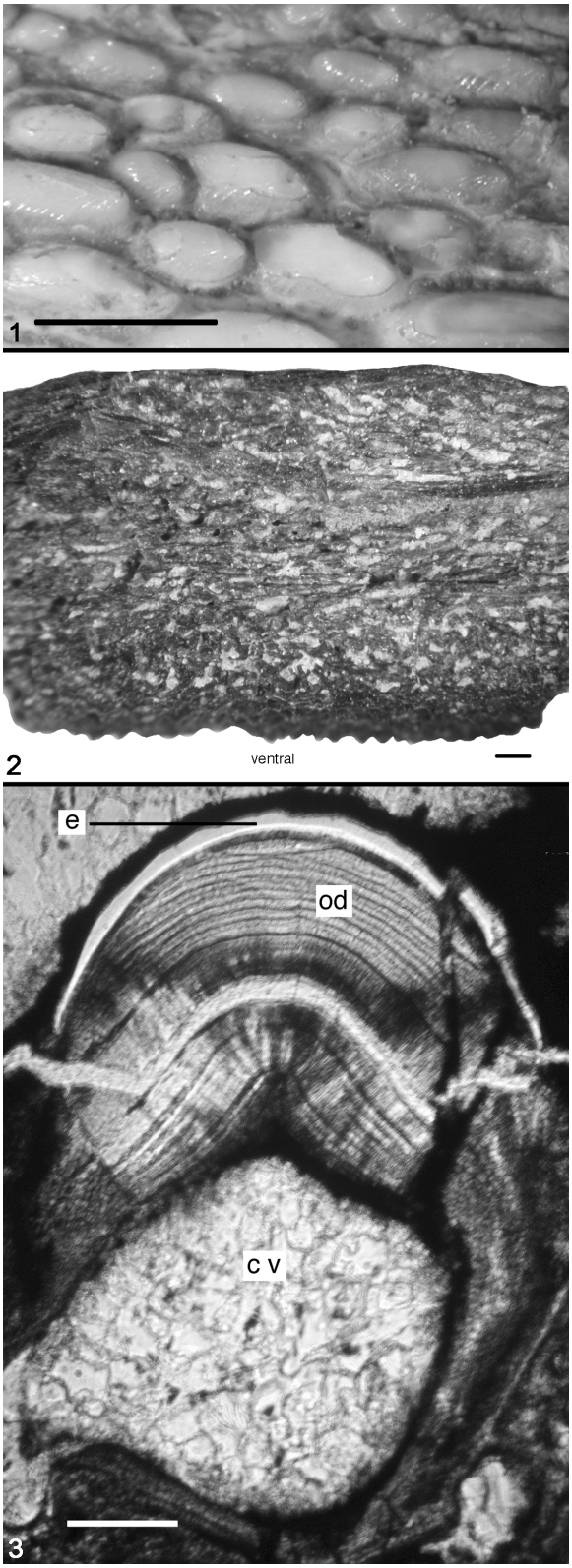

FIGURE 4. *Quayia zideki* Hunt, 2001 from NMMNH locality 1 (locality 2 of this study). **1**, Specimen NMMNH P-4685, close-up of marginal parasphenoid teeth. **2**, Specimen NMMNH P-4685. Note the high vascularization of the bone layer in the parasphenoid. **3**, Specimen NMMNH P-37820, a single parasphenoid tooth. The cavity (cv) is circular and very large. The orthodentine is well developed and covered by a thin enamel layer. Abbreviations: cv, cavity; e, enamel; od, orthodentine. Scale bars = 1 mm (except **3**: 0.3 mm).

Locality 3: Dying Grounds

Several bone fragments and tooth plates from Dying Grounds (Fig. 5) and a small scale have been examined. The teeth lack any radial

striation and are broadly based with an apical cap. There is some variation in the shape and arrangement of these teeth (Fig. 5.1-5.2). The specimens are brittle and not suitable for thin sectioning, but the internal structure is visible and uniform, highly vascularized by small canals and shows no replacement teeth (Fig. 5.2C).

The single scale preserved, however, is not determinate. It matches a general "palaeoniscoid" pattern of ganoin ridges running diagonally across the free scale surface, occasionally forking, and is not identifiable lacking more complete remains.

Locality 4: Lamy Bonebed

The single specimen (from L-1176) is a dentigerous fragment of a palatal bone. The external morphology of its inconspicuous, smooth and tiny teeth (about 0.1 mm in diameter in specimen NMMNH P-34232) indicates that the specimen may be a pterygoid or a coronoid of an otherwise indeterminate actinopterygian.

Locality 5: Upper Kalgary

Many tooth plate fragments bearing molariform and slender-conical teeth, other bone fragments, isolated teeth, and scales have been recovered from the second lowest locality considered in this study (L-1430). Preserved along with these fragments are numerous denticles. The teeth are either smooth and "molariform" (Fig. 6), or delicately striated and slender-conical with a transparent cap. No replacement teeth can be found in the thin sections. Scales associated with these finds have a smooth or uneven surface and occasional, faint ganoin ridges.

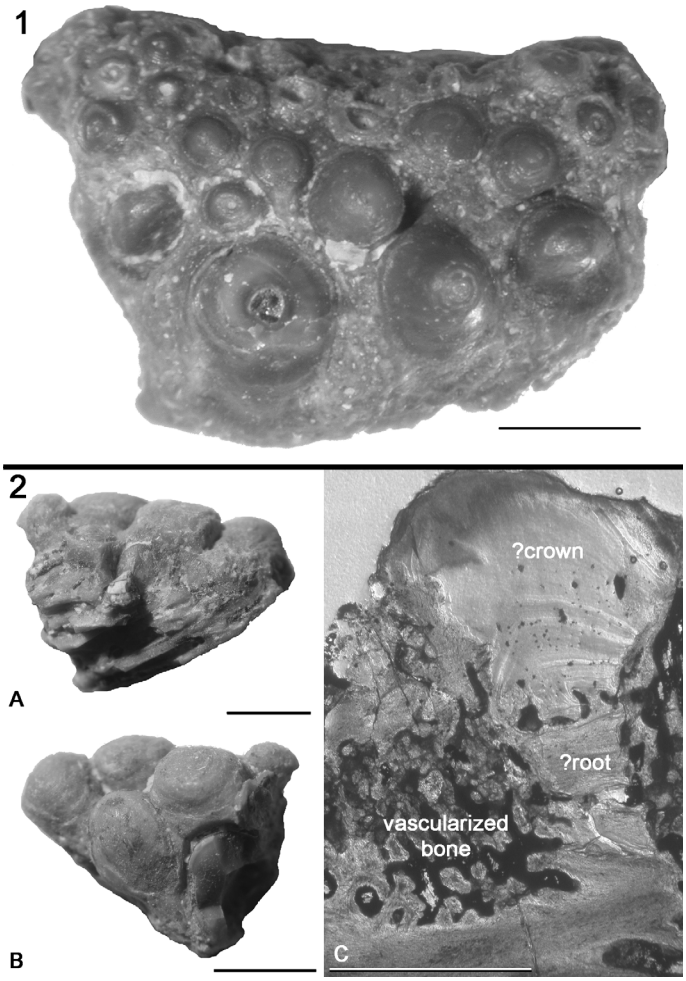

FIGURE 5. Dentigerous bones from Dying Grounds (locality 3 of this study). **1**, Specimen PEFO 20401, putative coronoid bone of an indeterminate osteichthyan. **2**, Specimen PEFO PFV-20416(a) in lateral (**A**) and occlusal (**B**) view and in thin section (**C**). The thin section of the same specimen reveals that there are no replacement teeth underneath the crowns. Scale bars = 1 mm.

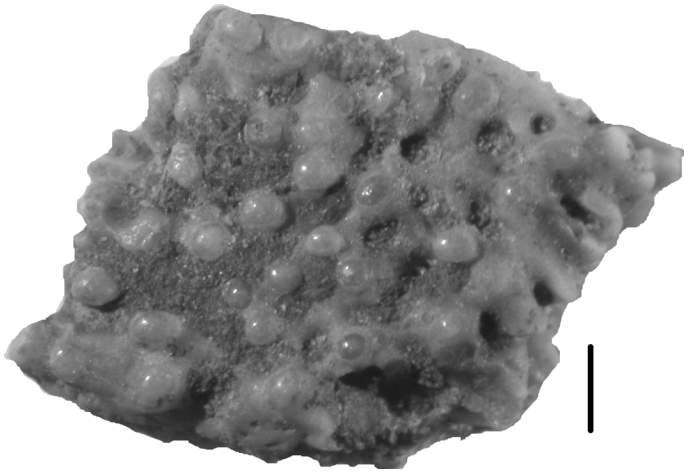

FIGURE 6. Specimen NMMNH P-26385: an indeterminate denticulate bone fragment from NMMNH locality 1430 (locality 5 of this study). Scale bar = 1 mm.

Locality 6: Lower Kalgary

The sample from this locality includes a number of morphologically diverse specimens and their morpho-histology provides much of the basis for the discussion in the following sections. These include both denticulate fragments and isolated teeth. Denticulate fragments bear teeth ranging from molariform to slender, but most have broad bases (NMMNH P-34398, Fig. 7.1). Some of these have distinct roots and ornamented crowns. Isolated teeth are present but not determinate below the level of Actinopterygii. Some of the denticulate plates possess denticles that look rather like tubercles and that may be recurved at their tips (Fig. 7.2-7.3) or are elongate (NMMNH P-34170) near the bone margin. The plates also differ in the density of their denticles. For example, specimen NMMNH P-30781 reveals high cusps and faint radial ganoin ridges on its denticles, but specimen NMMNH P-34189 consists of several bone fragments with tiny denticles. A shagreen of denticles is visible on the surface of one of the largest denticulate plates with spongy bone structure (see above, Fig. 7.3-7.4). In other fragments, there are smooth tubercles instead.

Unique Morpho-histology of the Denticulate Plates from the Chinle (Figs. 8-10)

When thin sections of representative specimens are examined, horizontal bone laminae delimit areas of high vascularization and the zone where multiple rows were developing. Up to five generations of denticles are present in some specimens. The "orthodentine" layer is very well developed and laminated, and this lamination appears to be confluent with the lamination in the surrounding bone. Unlike "true" teeth, no definite root or base can be delineated (Fig. 8.1-8.2). Osteocyte cell-spaces are abundant in the osseous matrix and cell processes are well developed (although less so in NMMNH P-37822). No distinctive lamina

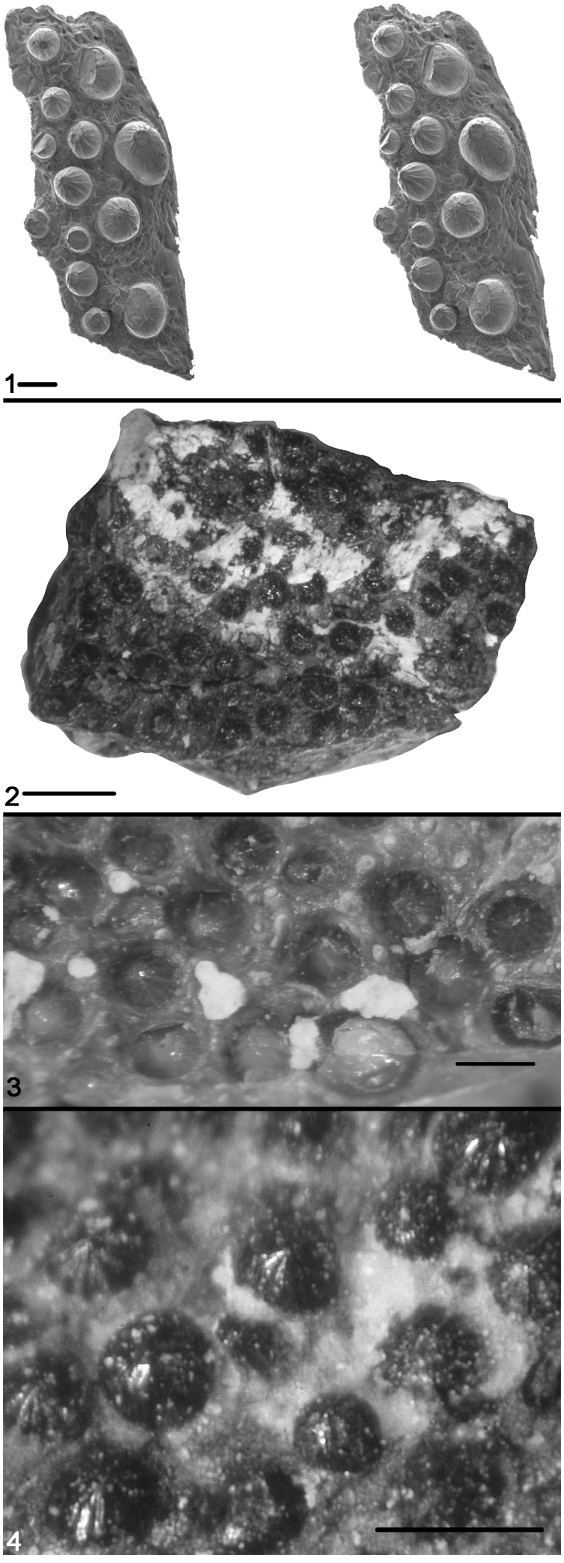

FIGURE 7. Various denticulate (?dentigerous) bone fragments from NMMNH locality 1312 (locality 6 of this study). **1**, Stereoimages of specimen NMMNH P-34398, an unidentified ?dentigerous plate. Scale bar = 1 mm. **2**, Specimen NMMNH P-34190, indeterminate denticulate plate. The "toothed" side of a thick bone showing tiny and well-spaced denticles. Scale bar = 0.3 mm. **3**, Specimen NMMNH P-34189, close-up showing some of the stellate denticles of an indeterminate bone. Scale bar = 0.1 mm. **4**, Specimen NMMNH P-34189, one of the larger denticulate plates used for thin sectioning, exhibiting small striated denticles. Scale bar = 0.5 mm.

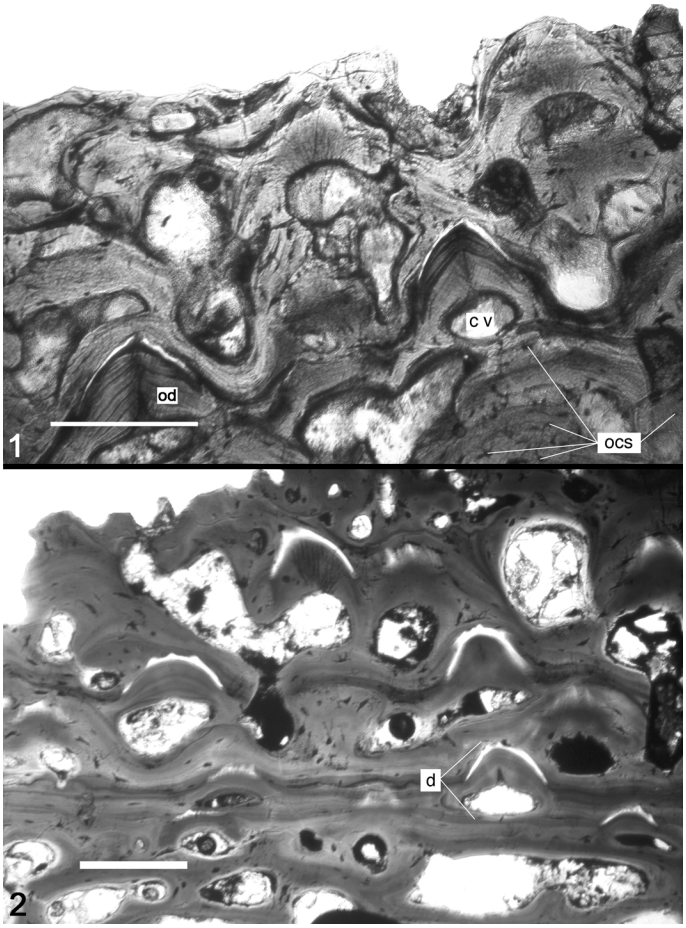

FIGURE 8. Thin sections of denticulate plates from NMMNH locality 1312 (locality 6 of this study) showing multiple (up to 5) replacement rows ("generations") of denticles. **1**, Specimen NMMNH P-37821, series of denticles in an indeterminate denticulate plate. **2**, Specimen NMMNH P-37822, series of "generations" of denticles in an indeterminate denticulate plate. Scale bars = 400 µm. Abbreviations: cv, cavity; d denticle; ocs, osteocyte cell-spaces; od, orthodentine.

separates the highly vascularized area from the zone of multiple rows of denticles. There is a large cavity (but relatively smaller than in parasphenoid teeth of *Quayia zideki*, NMMNH P-4685) below each denticle, tapering to a point apicad (compare Fig. 4.3 with Fig. 8.1-8.2). The denticles in NMMNH P-37821 show a peculiar apical cap that evidently lacks acrodin, even though the acuminate, tiny tip is missing in all denticles (Fig. 9.1-9.3).

To better understand the morpho-histology of these specimens, thin sections (NMMNH P-34189a-j) were made from 10 different denticulate plates that exhibit various internal and external morphologies. In summary, they vary in the following respects: first, the specimens differ in size and shape, and their denticles differ in morphology and arrangement. Second, the thickness of the bone does not necessarily correlate with the number of denticle sets, the presence of multiple rows of denticles, or the lamination or vascularization of bone. The plates (NMMNH P-34189) comprise fragments with only a single row of denticles (NMMNH P-34189b-c), rows variable in number (NMMNH P-34189a) or multiple (3-6) rows of denticles (NMMNH P-34189d-j). When a single row of denticles occurs, however, the denticles tend to be more densely placed, and in plates with several rows, the innermost denticles are the smallest whereas the broadest ones hem the surface of the bone. The enamel layer varies in thickness throughout its extent and exhibits an oblong pseudo-prismatic structure under transmittent light. Polished and etched enamel surfaces are devoid of basal lines under the scanning

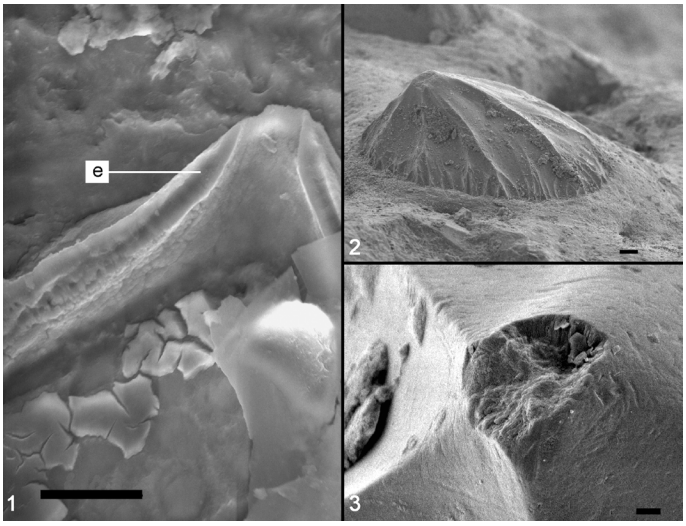

FIGURE 9. SEM close-up photographs of single denticles. **1**, Etched vertical thin section of the tip of a denticle in specimen NMMNH P-37821. Scale bar = 20 µm. **2**, Specimen NMMNH P-37820, indeterminate denticle in lateral view. Scale bar = 10 µm. **3**, Specimen NMMNH P-37820, close-up of apical tip of a denticle. Scale bar = 1 µm. Abbreviation: e, enamel.

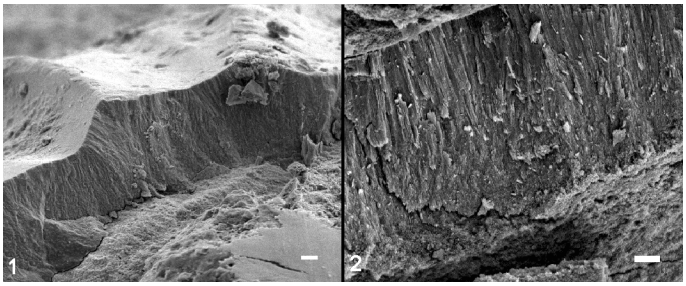

FIGURE 10. SEM photographs of enamel ultrastructure. **1**, Specimen NMMNH P-37820, fractured enamel layer of a single denticle. **2**, Specimen NMMNH P-34189, close-up of the fractured enamel layer showing outermost bundles of crystals running ~perpendicular to the denticle's surface. Scale bars = 1 µm.

electron microscope. Furthermore, specimen NMMNH P-37821 shows no evidence of crossed fibers (Figs. 9.1, 10.1-10.2; cf. Ørvig, 1978) as is typical of acrodin. It is possible, however, that the acrodin cap has broken off. In NMMNH P-37822, the vascularization is somewhat differently organized, indicating that it represents a different (indeterminate) dermal bone than specimen NMMNH P-37821.

INTERPRETATION AND COMPARISONS

Due to their unique histological nature, most fragmentary remains from the Chinle are not determinate at the generic level or even family level at present, although it is clear that these specimens do not represent either colobodontid or perleidid teeth. None of the investigated scales from localities 3 and 5 indicate the presence of Colobodontidae in the Chinle Group.

It is therefore appropriate to list here the new morpho-histologic features with regard to the respective samples from the various localities and to discuss the histological affinities in light of evidence from teeth and dermal bone of various better-known fish groups.

Locality 1: Actinopterygii gen. et sp. indet. (Denticle-like Teeth)

Both investigated specimens are actinopterygian denticulate plates, not yet identifiable to genus. The younger, larger teeth are accreted peripherally, whereas the older, smaller teeth are internal and not remodeled. The possible jaw bone in specimen NMMNH P-33113 suggests that this fragment may belong to an actinopterygian of not more than 100 mm total body length.

Locality 2: Osteichthyes gen. et sp. indet. (Teeth and Denticulate Plates)

The absence of conspicuous osteocyte cell-spaces in the bone, the lack of acrodin, and the presence of irregular basal lines in the enamel layer, suggest affinities with certain actinistian or derived actinopterygian taxa.

Locality 3: Actinopterygii gen. et sp. indet.

None of the bone fragments or teeth bear any resemblance to colobodontid remains, but one specimen (PEFO 20401; Fig. 5.1) is distantly reminiscent of teeth found in the adult semionotid *Paralepidotus* from the Norian of northern Italy – although at a much smaller scale. Unfortunately, the tooth ultrastructure in a second, fragmentary dentigerous bone could not be examined in thin section because it was too brittle. The single scale preserved probably belongs to an otherwise indeterminate palaeoniscoid.

Locality 4: Actinopterygii gen. et sp. indet.

The single specimen from locality 4 examined, a palatal fragment with teeth, pertains to an indeterminate actinopterygian.

Locality 5: Actinopterygii gen. et sp. indet.

Many of the fossils from locality 5, including many tooth plate fragments, bone fragments, and denticles, as well as many of the scales, probably pertain to an indeterminate actinopterygian. The superficial scale structure is typical of palaeoniscoid scales.

Locality 5: Actinistia gen. et sp. indet.

At least some bone fragments (dentigerous and denticulate plates) and teeth represent remains of coelacanths (cf. *Quayia zideki*).

Locality 6: Osteichthyes gen. et sp. indet.

This sample is the most diverse and the majority of these remains include indeterminate denticulate plates (some with multiple generations of denticles) and isolated teeth. None of the investigated remains bear resemblance to the teeth of colobodontids, and it is not clear whether some of the fragments even represent remains of actinopterygians.

Comparison with Colobodontids

In contrast to previous workers, our survey suggests none of the studied enigmatic "molariform teeth" from the Upper Triassic Chinle Group are teeth or dentigerous bones of colobodontids. Colobodontidae (erroneously synonymized with Perleididae) are widespread in the Early-Middle Triassic and the claim of their occurrence in the early Late Triassic Southwest is legitimate (Mutter, 2004). Pioneer work on colobodontids found in central Europe was originally also established on isolated teeth in mid-1800. These Chinle fossils represent dermal denticles with a unique internal structure (but not "functional teeth") embedded in dermal bone. Smaller, more basally placed denticles are embedded in laminated bone, and an increase in denticle size normally occurs from the basis apicad when multiple rows are present, suggesting centripetal growth. No traits suggesting external wear or major internal remodeling or resorption were found in the denticulate plates, and the dentine layer of the denticles is not delimited from surrounding bone matrix. Unequivocally dentigerous, larger plates can easily be differentiated from *Colobodus bassanii* and allied taxa by the lack of a stellate ornament, an apical acrodin cap, or both (see below, Fig. 11.1-11.2).

Many of these dentigerous plates are not identifiable to lower

TABLE 1: Morphological and histological comparative data of externally similar molariform teeth.

Taxon	Size of teeth	External morphology	Histology	Hypermineralized Tissue (Enameloid)	Replacement Teeth/ Denticles
Colobodus cf. *bassanii*, Colobodontidae, PIMUZT 5253	up to 6mm	radial ridges, apical wart	moderately vascularized	thick layer (circumverrucal	one row, teeth not fully developed
Nephrotus chorzowiensis Meyer, 1847	up to 1.5mm	radial ridges, apical wart	?	thin layer with large acrodin cap	?
Bobasatrania sp. SMNS 59184	about 0.3mm	smooth, no wart	teeth with cavities densely set	thin layer, extensive acrodin	several generations, teeth "stacked"
Paralbula casei Blake, 1940 (phyllodont)	0.1-0.3mm	hemispherical, blunt, radiate ornament, wart	basilar foramen	thin layer, entirely consisting of acrodin (?)	several generations, strictly alternating
Chinlea sorenseni Elliott, 1987	?	low-crowned, conical	?	?	?
Spermatodus sp. Meinke, 1982	heterodont	either smooth or with ridges	?	?	?
Whiteia sp. UALVP 46583	up to 1.5mm	low-crowned, conical, blunt	highly vascularized	very thin layer, no acrodin cap	none
Quayia zideki NMMNH P-46585	up to 0.3mm	radial ridges	highly vascularized	thick layer, no acrodin	none
Enigmatic tooth plates from Chinle, i.e., Fig. 5	up to 2mm	smooth	vascularized by narrow canals	present, extension of acrodin, unknown	none
Enigmatic denticulate plates from Chinle, i.e. Figs. 6-7	up to 0.3mm	radial ridges or smooth	"denticles" with cavities densely set	thin layer, no acrodin?	several generations, denticles

All specimens are molariform teeth found in Early Mesozoic fishes and in the "phyllodont" Late Mesozoic species *Paralbula casei*. All specimens used in this study are listed under material and methods, literature was used as cited. Note that tooth/bone histology of certain coelacanths is particularly poorly known. Denticulate plate histology from Chinle is unique — unparalleled by any known Late Paleozoic/Early Mesozoic taxon.

taxonomic levels because stellate ornamentation on the surface of denticles and teeth overlying dermal bone externally is widespread, a primitive feature and therefore of little diagnostic value. All "tooth plates" from the Chinle Group previously believed to belong to *Colobodus* are much smaller in size. On average, their diameter is up to 30 times smaller than the size of comparable teeth in colobodontids. A central wart (tip) may be present in some teeth but they clearly lack a colobodontid-like acrodin cap (see below). Furthermore, in colobodontids, the molariform teeth with stellate ornament are usually regularly arranged on the bone surface, and typically grade from smaller to larger peripherally (Mutter, 2002). This characteristic is rarely observed in Chinle specimens, which typically bear tiny, ornament-rich denticles. In addition, it is highly unlikely the difference in absolute tooth size and the absence of scales of *Colobodus* are due to preservational circumstances or due to methods of sampling (collecting bias). Respective specimens resemble each other in bone and denticle structure: one or multiple rows of denticles (up to 5 "generations") are present below the outermost row, superficially reminiscent of "phyllodont" tooth replacement (see below).

Despite the similarity in stellate ornament of true colobodontid teeth and some of the specimens in question (compare Figs. 7 and 11, and Mutter, 2004: fig. 1), the Colobodontidae do not possess "multiple, superposed sets of replacement teeth" as suggested by Hunt (2001). Indeed, Figures 12.1-12.3 demonstrate that no more than one set of replacement teeth is formed below the dermal jaw margin and in the ectopterygoid of *Colobodus* sp. Nevertheless, the histology of the teeth themselves differs considerably in the sectioned specimens from the Chinle and in known colobodontids (Fig. 12.3). Colobodontid teeth possess a distinctive acrodin cap, an apical tip of the pulp cavity that does not taper to a point but is slender-elongate instead of round. The pulp cavity ends comparatively deep below the apical acrodin cap, which covers the central wart that is superficially visible (see also Guttormsen, 1937; Ørvig, 1978). The orthodentine layer (Fig. 12.3, od) is accordingly well developed in *Colobodus*. As mentioned previously, some teeth in these enigmatic denticulate plates from the Chinle possess a central wart (e.g., specimen PEFO-20414) but we have not found any evidence of a central acrodin cap as in *Colobodus* and many other actinopterygian teeth (compare Figs. 8 and 9.1 with 12.3). Instead, these "teeth" exhibit a peculiar histology, not in accordance with their superficially colobodontid-like external appearance. Table 1 summarizes the results of our morpho-histologic comparisons with various Triassic fish groups discussed in the following paragraphs.

Nephrotus chorzowensis Meyer, 1847 from the lower Muschelkalk (Lower Triassic) of Chorzow (Poland) may be a member of Colobodontidae (Mutter, 2002, 2004) but differs considerably from the specimens under investigation in having a large acrodin cap.

Comparison with Non-Colobodontid (Non-Perleidid), Penecontemporaneous Actinopterygians

Tooth plates containing teeth of consecutive generations have been reported in the Early-Middle Triassic basal actinopterygian *Bobasatrania groenlandica* and the Late Permian palaeonisciform ?*Schaefferichthys* sp. (Ørvig, 1978; Johnson and Zidek, 1981). In the latter taxon, the enamel cover is smooth externally and consists of plain acrodin; the overall histology of the teeth and their arrangement bear no resemblance with any of the investigated specimens from the Chinle.

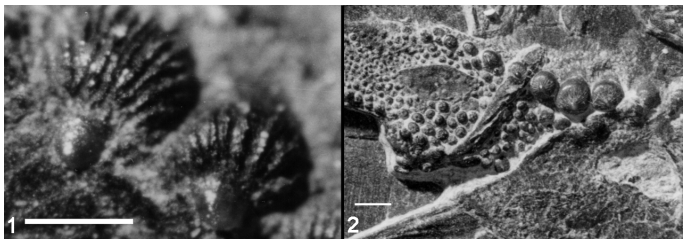

FIGURE 11. Morphology of colobodontid teeth. **1**, *Colobodus* cf. *C. bassanii* (specimen PIMUZ T 3010); detail picture of just erupting, tiny crushing teeth found in the ectopterygoid; note that the striation and the apical acrodin tip are very conspicuous at this tooth size and smaller (scale bar = 0.5 mm). **2**, Colobodontidae gen. et sp. nov. (specimen PIMUZ T 588); close-up of non-abraded typical crushing teeth on a pterygoid bone. Scale bar = 3mm.

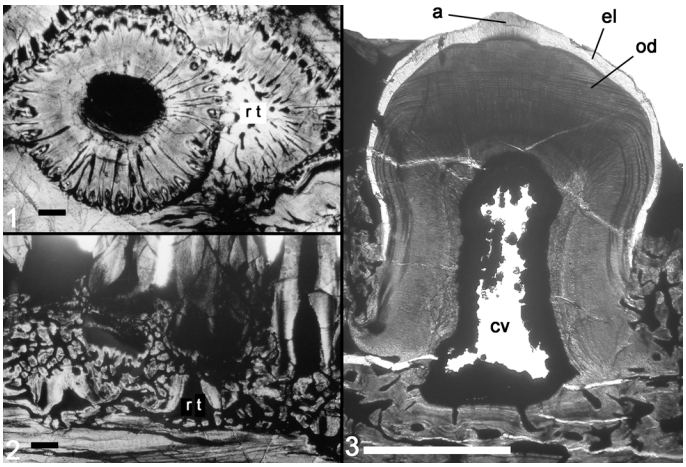

FIGURE 12. Histology of colobodontid teeth. **1**, *Colobodus* sp. nov., specimen PIMUZ T 24, cross section through the base of a large ectopterygoid tooth (section P II 012). **2**, *Colobodus* sp. (specimen PIMUZ T 5253, thin section P II 014). Vertical thin section of the anterior region of the dentigerous border of the maxilla (figured upside down). Note positions, orientation, and stage of development of non-functional "erupting" teeth in the maxilla. **3**, *Colobodus* sp., specimen PIMUZ T 1710 (thin section 1). Vertical thin section of a crushing tooth. Note the presence of acrodin (a) and the shape of the cavity (cv). Abbreviation: a, acrodin; el, enameloid layer; cv, cavity; od, orthodentine; rt, replacement tooth. Scale bars = 1 mm (except **1**: 0.2 mm).

Bobasatrania possesses a single, relatively large median tooth plate in both the lower and upper jaws. The dentine layer in each tooth is delimited from the matrix within true sets of multiple rows of teeth (Fig. 13). Thus, only the general arrangement resembles that of Chinle specimens but the teeth differ in their shape, pulp cavity, and thickness of the enamel (acrodin) layer (Fig. 13.1-13.2, Table 1).

Comparisons with Dentigerous and Edentulous Osteichthyan Bone

Our interpretation of many of the fragmentary denticulate plates from the Chinle is that they resemble non-toothed dermal bone rather than dentigerous bone. This hypothesis is supported by the presence of the more or less highly vascularized denticulate layer in osteichthyan dermal bone.

However, investigated dermal bones in colobodontids, coelacanths and in an unidentified osteichthyan lack well-developed odontodes and/or "generations" of denticles almost entirely (Fig. 14). The dermal bone of all 3 groups shows large cavities, indication of high vascularization. The coelacanth bone shares a high degree of vascularization with multiple cavities and one large cavity below the odontode with a thin, apical,

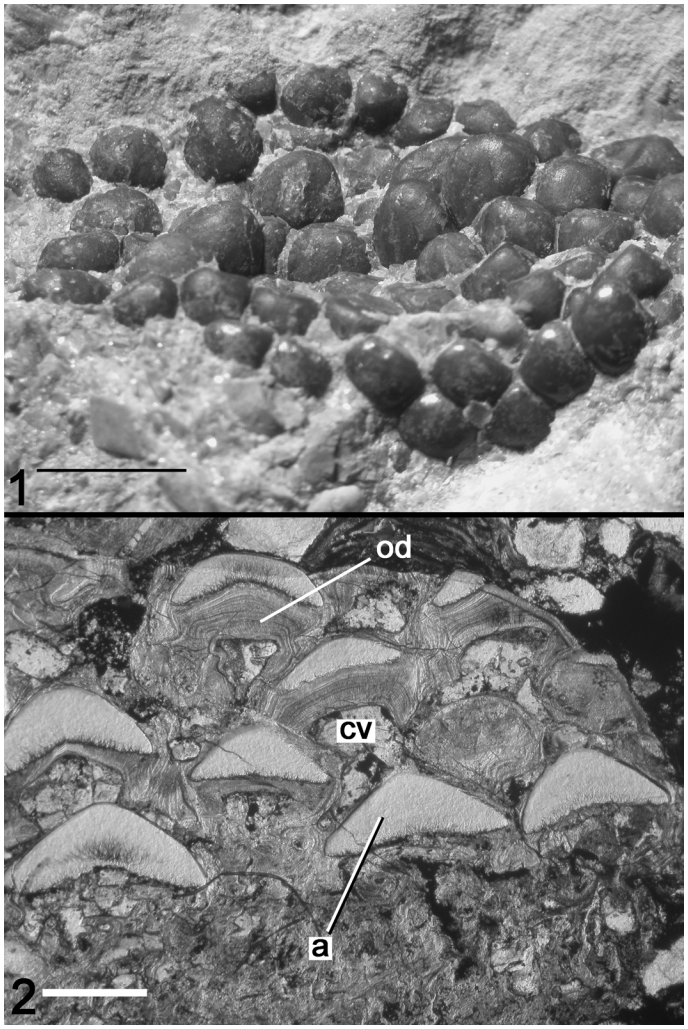

FIGURE 13. Morpho-histology of crushing teeth of *Bobasatrania* sp. 1, Specimen SMNS 87971: a dentigerous tooth plate in occlusal view. Scale bar = 3 mm. **2,** Thin section through specimen SMNS 59184, showing the densely spaced teeth with thick orthodentine and acrodin layer (a). Abbreviations: a, acrodin; cv, cavity; od, orthodentine. Scale bar = 0.5 mm.

highly mineralized layer (Fig. 14). In colobodontid dermal bone, remnants of previous growth stations are visible in thin sections (Fig. 14.1).

The phenomenon of a non-columnar arrangement of teeth of consecutive generations is also reminiscent of Ørvig's (1978, p. 300-302, fig. 12) model of consecutive generations in the dermal bone, a common occurrence in various lower vertebrates, including for instance, holoptychiids or coelacanths such as Recent *Latimeria* (see below). However, the peculiar histologic structure disclosed in these denticulate plates was hitherto unreported.

Comparison with Selected Osteichthyans, Particularly Coelacanths

Judged from their external morphologic appearance, some of the larger fragments with teeth of variable size represent fragmentary (crushing and non-crushing) actinopterygian tooth plates but cannot be identified more precisely. The smaller fragments with uniformly shaped, densely placed, tiny, and stellate "phyllodont" denticles are more likely to represent unidentifiable dermal plates. These small denticles resemble *Quayia zideki* (specimen NMMNH P-4685) in single-tooth structure (see below) but the parasphenoid of the latter taxon has more distinctly organized teeth. Coelacanths are not known to possess multiple rows of teeth or denticles (see below), and should easily be distinguished by

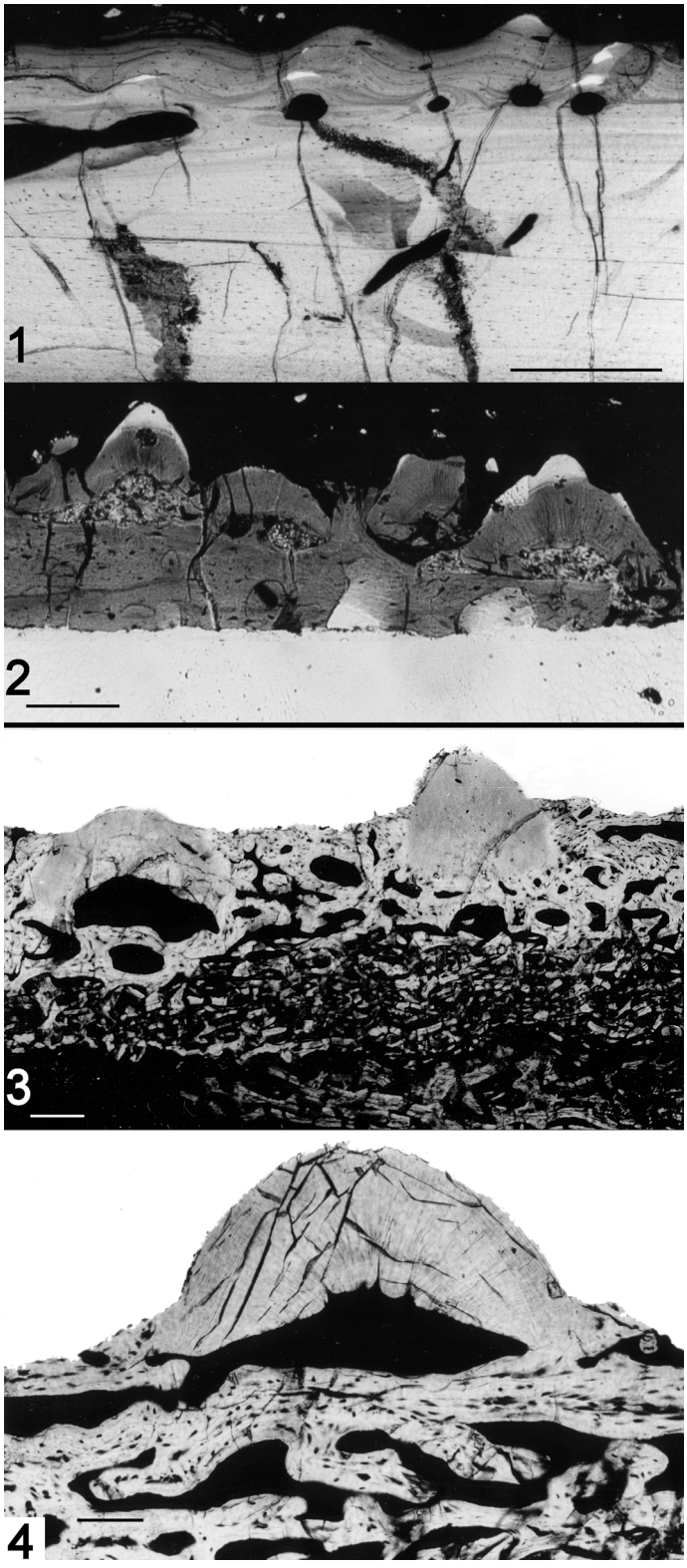

FIGURE 14. Histology of dermal bone structure in Triassic osteichthyans. **1,** *Colobodus* sp., specimen PIMUZ T 5253 (P I 027), vertical section through the parietal. Scale bar = 400µm. **2,** Osteichthyes gen. et sp. indet. from the Besano Formation, specimen PIMUZ T 2538 (P I 019), vertical section showing the internal structure of an indeterminate dermal bone fragment. Scale bar = 100 µm. **3,** Coelacanthidae gen. et sp. indet., specimen PIMUZ T 1327 (P II 037), vertical section through indeterminate dermal bone. Scale bar = 100 µm. **4,** Coelacanthidae gen. et sp. indet. Close-up of thin section P II 037. Scale bar = 50 µm.

more or less parallel lines at the base of the enamel layer.

In several Triassic genera of coelacanths, the presence of crushing teeth is no surprise (e.g., Schaeffer, 1941, 1948, 1967). According to Forey (1991, 1998), coelacanth diversity does not peak in the Triassic (but see Schultze, 2004), but, interestingly, crushing dentitions are widespread at that time only. Furthermore, the common coelacanth in the Chinle, *Chinlea sorenseni*, also shows adaptations for durophagy (Schaeffer, 1967, p. 325 and fig. 14) and persists from the Otischalkian to the Apachean (Johnson et al., 2002). Remains of coelacanths are present even in localities where body fossils are sparse (e.g., in the Bell Springs Formation in northeastern Utah and northwestern Colorado, Huber et al., 1993). Unfortunately, none of the crushing dentitions of *Chinlea* is preserved *in situ*, and no appropriate isolated material has been available for sectioning (Table 1). The most complete specimen (described by Elliot, 1987) from the Dolores River Canyon (Bedrock, Colorado), has no *in situ* teeth visibly preserved (D. Elliott, personal commun., 2003). Although substantial studies on coelacanthid dentitions and dermal denticles have been conducted (Schultze and Cloutier, 1989; Forey, 1991, 1998; this study), remarkably little information on the ultrastructure and on different types of teeth is available (see also Smith, 1978).

We made and examined several thin sections of the parasphenoid, several branchial bones and unidentified dentigerous bones of *Whiteia* sp. from the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation in western Canada (Smithian, Early Triassic). The teeth exhibit a variable external morphology and vary greatly in size but the histologic study reveals a consistent pattern: no replacement teeth, slender-conical pulp cavities, and a thin enamel layer (see Table 1).

The "spongy," highly vascularized bone developed in the larger, denticulate plates from the Chinle, however, suggests macroscopic coelacanthid affinities; large and numerous cavities open into the basal bone layers and are separated by comparatively slender walls. In contrast, the dentigerous bones are rather "dense" in colobodontids; the cavities are more stringently localized and invest the bone with a less porous appearance (Fig. 14). As can be seen from the thin sections, many enigmatic tooth plates from the Chinle are significantly more vascularized than the pterygoid or the dentigerous bones of *Whiteia* sp. and an unidentified coelacanth from the Middle Triassic of southern Switzerland (Anisian/Ladinian boundary, Besano Formation) (Fig. 14). The coelacanth *Spermatodus* sp. from the Lower Permian of Admiral (Archer County, Texas) also possesses a heterodont dentition: both smooth-conical and ornamented-spheroidal teeth are found *in situ* on the pterygoid (Fig. 15.1-15.2) but, unfortunately, none of these teeth are suitable for histologic examination (see Table 1).

Meinke (1982: p. 621) briefly reported on dermal denticles, conical teeth, and a "complete gradation from teeth to denticle shapes" in the Permian coelacanthid *Spermatodus pustulosus*. However, according to Meinke (1982), the latter plates only possess one layer of "dermal denticles," and both (teeth and denticles) have dermal enamel in *Spermatodus* (as in *Latimeria*, see Shellis and Poole, 1978; also Grady, 1970).

Stensiö (1921) described Early Triassic coelacanths with heterodont dentitions (especially *Scleracanthus*) and referred to their tiny crushing teeth as reminiscent of *Colobodus* from the Middle Triassic of the Besano Formation. Interestingly, he noted that these coelacanth teeth could easily be misidentified as "*Colobodus*" when recovered as isolated specimens (Stensiö, 1921, p. 102).

To our knowledge, no superposed replacement teeth have ever been reported for coelacanths; there is a single functional tooth row in the parasphenoid of *Quayia zideki* (NMMNH P-4685) and in the basibranchials of *Whiteia* sp. (UALVP 46583 T1-12). In single tooth-histology alone, some of the enigmatic "tooth plates" we examined (e.g., NMMNH P-34189) are nearly identical to teeth of *Quayia zideki* (see Fig. 4.3), except for their much smaller size and the lack of irregular lines in the enamel (Table 1).

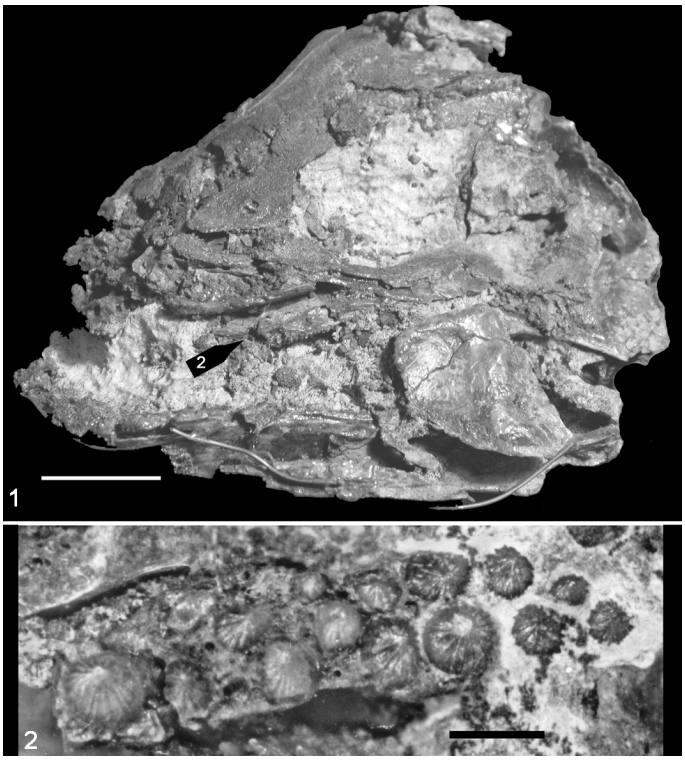

FIGURE 15. Teeth with stellate ornament in the coelacanth *Spermatodus* sp. **1,** Specimen AMNH 4612, the skull in lateral view. Arrow indicates *in situ* position of tooth plate (enlarged in **2;** scale bar = 0.5 mm). Scale bar = 20 mm.

Wilson (1949) had originally concluded that isolated, phyllodont and molariform tooth-bearing plates from the Permian Vale Formation pertain to a large coelacanth. His interpretation was challenged by Johnson and Zidek (1981) because no replacement teeth could be found in the basibranchials of Early Triassic coelacanths from east Greenland (according to an unpublished study by Eigil Nielsen, Copenhagen). We were also unable to confirm the presence of replacement teeth in Early-Middle Triassic coelacanth teeth from the Sulphur Mountain Formation or from the Besano Formation. Johnson and Zidek (1981) concluded that crushing teeth in *Spermatodus* are "toothed rather than tooth plate-bearing bones." However, the proposal that "phyllodont tooth plates" from the Chinle in fact represent coelacanth tooth plates is not iron-clad, either: the enamel layer in coelacanth teeth characteristically appears laminated basally, regardless of relative tooth size (Smith, 1978). Indeed, extremely regular, parallel lines can be observed in the enamel of *Whiteia* sp. In the enamel of *Quayia zideki*, however, there are irregular basal lines. The etching of the enamel layer had a variable effect in one enigmatic denticulate plate (specimen NMMNH P-34189); it produced an oblong, prism-like structure but no lamination parallel to the tooth surface was found. As a result, small coelacanth teeth – although externally and in single-tooth histology strikingly similar – could not be shown to be arranged as multiple sets of replacement teeth and are readily distinguished by enamel microstructure.

Comparison with "Phyllodonts"

Estes (1969a, b) described various types of teleost phyllodont tooth plates with conspicuous differences in tooth arrangement and morphology, and with earliest occurrences in the Upper Cretaceous of New Jersey and Alberta. "Phyllodont" tooth plates were also described from several Upper Paleozoic formations in the southern U.S. (Johnson and Zidek, 1981). The occlusal outline of the Upper Paleozoic phyllodont tooth plates are distinctively diamond-shaped and have not been preserved in any of the Chinle specimens. As seen from the extensive acrodin caps in teeth and associated platysomid remains in specimen OUSM 00509 (Johnson and Zidek, 1981, text-fig. 1H), the tooth plates from the Permian East Manitou site in Tillman County, Oklahoma, are undoubtedly referable to an actinopterygian.

Despite the differing morphology, 4-6 superposed sets of denticles, distantly reminiscent of replacement teeth in phyllodonts, are also present in several plates from the Chinle Group. All of those species but *Paralbula casei* Blake, 1940 are easily differentiated on histologic grounds from the specimens studied here. In the 11 specimens Johnson and Zidek (1981) sectioned, phyllodont teeth are invariably densely and regularly arranged, the structured acrodin cap represents the thickest of all layers, the apical enamel layer is very thin, and the "dentine" layer is intermediate in thickness (Table 1). The pulp cavity reaches far into the tooth to form a cone-like pouch. Again, although some teeth bear superficial resemblance to several of the specimens investigated here (densely set teeth, acute-conical tips, broad bases, smooth surfaces with well-developed enamel caps), these features occur, alone or together, in various actinopterygian fish groups (Ørvig, 1978). Single tooth histology of *Paralbula casei* from the Miocene superficially resembles the denticles described here relatively closely (radiate surface sculpture and thin enamel layer) but this taxon is only known by six tooth plates from the Late Mesozoic/Early Cenozoic, and the teeth possess a conspicuous basilar foramen (see Table 1).

CONCLUSIONS

The investigated enigmatic remains represent (often) denticulate and (rare) dentigerous plates whose common denominator is a stellate ornament. The denticulate plates belong to as-yet unidentified osteichthyans, and this morpho-histologic study reveals their unique internal structure for the first time. With regard to the extensive collection of fossil remains from the Chinle, these findings are of considerable importance for future studies on its fish fauna. We feel confident to exclude, on the basis of this study, tooth plates of colobodontids (and perleidids) from the array of suitable candidates for identification for any of these fragmentary remains from the Chinle Group. Thus, there are no records of "colobodontids" or "perleidids" from the Chinle, and indeed colobodontids remain restricted to the Middle (probably Early) marine Triassic. The denticulate plates show a peculiar histology, and are not associated with any colobodontid scales in any locality of the Chinle Group. Tiny denticles (previously called "teeth") ornamented by radial ridges (stellate ornament) occur in diverse osteichthyan groups that are not closely related and therefore not necessarily diagnostic. At present, redundant material of unambiguously identifiable, more complete fishes suitable for destructive preparation and investigation is not available. Yet a detailed morpho-histologic study of identifiable coelacanth, palaeoniscoid, redfieldiid and semionotid material might reveal whether certain teeth and denticulate plates can be identified as to belonging to one of the previously described more complete freshwater fishes from the Chinle Group.

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